THE FEEDING MECHANISM IN THE SAND DOLLAR MELLITA SEXIESPERFORATA (LESKE)

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MacGinitie and MacGinitie (1949) give the following account of feeding in the scutellid echinoderm *Dendraster excentricus* (Eschscholtz) (p. 237): "The spines on the upper side of the sand dollar are club shaped and are covered by cilia. These cilia create currents that flow from the direction in which the animal is moving toward what could be called the posterior edge. . . . As the currents flow through these spines, little eddies are created at the posterior sides of the spines. These eddies allow tiny particles and organisms to become trapped in mucus that is secreted onto the surface of the spines. This mucus goes downward and is led into tiny tracts to unite with others. These in turn unite again, passing around the edge to the underside, until near the mouth five tracts or strings of mucus feed directly into the mouth of the sand dollar." This appears to be the only available account of feeding in the Clypeasteroida. Hyman (1958) studied the five-lunuled sand dollar *Mellita quinquiesperforata* (Leske), but was unable to elucidate the feeding mechanism. The present paper describes observations made on another of the lunuled sand dollars, *Mellita* (*Leodia*) *sexiesperforata* (Leske), and shows that it is a ciliary mucus feeder collecting particles on the aboral surface and transporting them through the lunules and around the margin of the test to food tracts on the oral surface.

M. sexiesperforata is common in certain shallow water sandy areas around Jamaica and normally lives either in the surface layer of the sand, so that its outline is discernible from above, or else buried in the sand very close to the surface. The animals used for these observations were collected on the Port Royal Cays and observations were made both in the aquarium and in dishes under a microscope.

Morphology

Figure 1 shows an individual in both oral and aboral views. The size of the animals varies considerably, fully grown animals being about 70 to 80 mm. in diameter. In surface view the animal has a roughly pentagonal outline and its surface is pierced by six slit-like lunules: five of these are in the ambulacral areas, the sixth or anal lunule is interambulacral and marks the posterior side of the animal. The anterior side of the test is markedly pointed. Both aboral and oral surfaces are densely clothed with short spines which are described below. On the aboral side of the only other structures visible are lunules, petaloids, and gonopores. On the oral surface the mouth is central and the anus lies posterior to it, just on the edge of the anal lunule. Leading away from the oral margins of the five ambulacral lunules are a number of broad *food tracts*: one of these, the radial tract, leads straight from the inner tip of the lunule to the mouth, the remainder run laterally from the lunule and terminate in the *ambulacral* or *food grooves*. These are deep but narrow grooves, a pair to each ambulacral area running into the mouth; the two members of a pair form a petaloid outline and unite just before reaching the mouth. The food tracts of the anal lunule are less well developed and discharge laterally to the ambulacral grooves of the two neighboring lunules.

Figure 2 shows the profile of a sagittal section through the test and shows that it is thin around the margin and dome-shaped in the center; the anterior margin is thicker than the posterior margin. The mean measurements for the ten individuals of 60 to 65 mm. diameter are:

Anterior margin:	1.8 mm.	±0.04
Central dome:	5.9 mm.	±0.49
Posterior margin:	1.0 mm.	±0.01

It is significant that the animal progresses through the sand with the anterior and thicker margin foremost.

Podia

On the oral surface there are dense concentrations of podia around the periphery of the test, around the margins of the food tracts and in the lunules. They are less dense on the remainder of the ambulacral areas and are absent from areas

FIGURE 1, a. The aboral surface of a living *Mellita sexiesperforata*. The anterior end is towards the top of the picture. The club-shaped spines appear as minute spots all over the surface of the animal. Notice that the peripheral (ambulatory) spines are more dense anteriorly than posteriorly. The ring of protective spines can be seen clearly around the margin of each lunule.

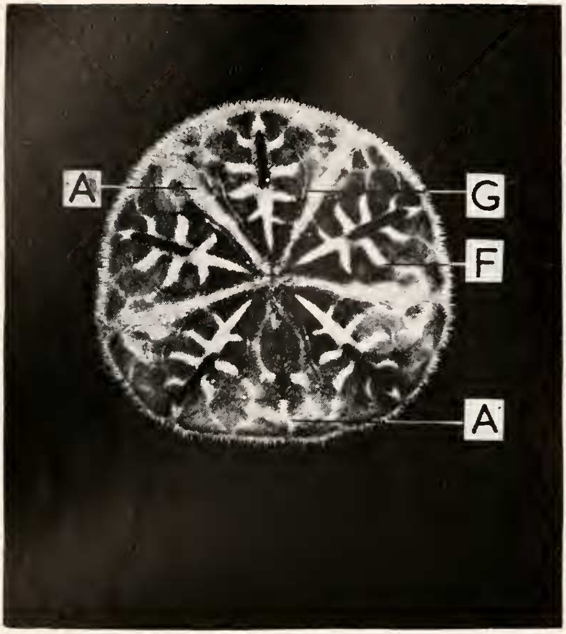

FIGURE 1, b. The oral surface of a living *Mellita sexiesperforata* stained for two minutes in toluidine blue. Orientation as in Figure 1, a. The stain is taken up by podia and other structures, and was used to improve contrast. The mouth is central and the anal papilla appears as a black spot between it and the anal lunule. The anal spines between anus and mouth are just visible. A = Ambulatory spine; F = Food tracts; G = Food (ambulacral) grooves.

with ambulatory spines. On the aboral surface there are only a few scattered podia. When extended the podia are very long and thin with a slightly swollen tip and poorly developed sucking disc. They function exclusively as an accessory food collecting device (see below) and do not appear to play any part in locomotion.

Spines

There are four principal types of spine. On the oral surface ambulatory and non-ambulatory spines can be distinguished. Ambulatory spines are confined to five locomotory areas in the interambulacra of the oral surface. In the anal interambulacrum they form a transverse group behind the anal lunule, in the other four interambulacra they form a radially disposed wedge-shaped group (Fig. 1b). These spines, which are long and thick ($1300\,\mu \times 85\,\mu$) normally have a rounded tip but in many spines the tip is abraded into a roughened end (Fig. 3, A); their

FIGURE 2. Profile of *Mellita sexiesperforata*. The anterior end is toward the right of the picture.

function appears to be entirely that of locomotion. Similar spines are found all around the margin of the test but they are almost twice as thick ($1300\,\mu \times 160\,\mu$); they are densely arranged anteriorly and more scattered posteriorly. Their extra thickness is probably correlated with stresses set up during movement through the sand in a horizontal direction. Non-ambulatory or protective spines of the oral surface are shorter and thinner ($430\,\mu \times 30\,\mu$) than ambulatory ones and are often bent near the middle of their length (Fig. 3, B); they cover all the remaining areas of the oral surface. Similar spines are found in the lunule and on the aboral margin of the lunule they form a protective ring projecting up higher than the other spines of the aboral surface; here they prevent very large sand particles from entering the lunule and blocking it.

On the aboral surface there are two types of spine distributed together all over the animal. The larger of these are club-shaped spines which move the

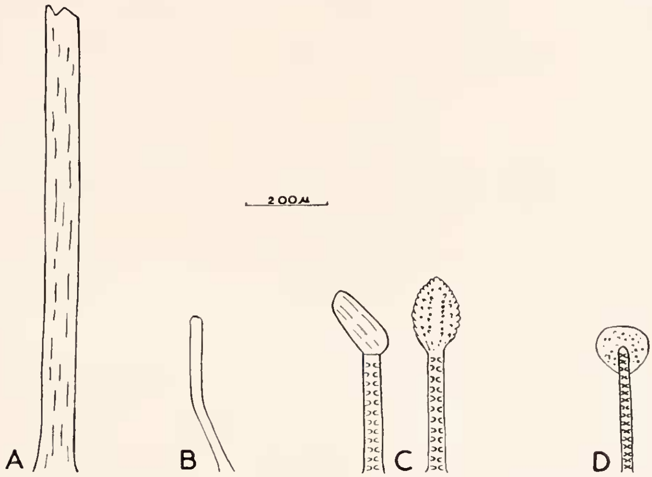

FIGURE 3. The principal types of spine found in *Mellita sexiesperforata*. A = Ambulatory spine with abraded tip. B = protective spine of oral surface. C = Two views of club-shaped spines of aboral surface. D = Aboral miliary spine.

sand grains posteriorly over the aboral surface (Fig. 3, C). The club-shaped head of these spines is set at a slight angle to the stem and its tip is oriented toward the margin of the test. The others or miliary spines (Fig. 3, D) are shorter than the club-shaped spines and are characterized by having a sac-like swelling on the tip; this sac contains yellowish granules which stain darkly with toluidine blue. The epithelium at the base of the cilia on these spines stains purple with the same stain and it seems plausible therefore to suggest that these spines are the principal site of mucus secretion. Miliary spines also occur on the inner walls of the lunules and along the food tracts of the oral surface; the latter have a smaller sac than those of the aboral surface or lunule.

As well as these four main types of spine there is a group of very large spines forming a circle between the mouth and anus and with their tips overarching the anus. They play an important part in preventing feces from entering the mouth.

These spines are in three groups: seven or eight very long ones (up to 5 mm. in length) form a group nearest to the anus, outside these there are ten to twelve of intermediate size, then a group of many smaller ones forming an outer ring next to the mouth. (Fig. 1b).

Cilia

Cilia are confined to the epithelia of the spines and are found on only one side of the stem. This side of the stem is here referred to as its back and the cilia beat in such a way as to drive a horizontal current from it in a backward direction. On the aboral surface the club-shaped spines have dense ciliation at the base while the miliary spines have dense ciliation along the whole length of the stem. The club-shaped and miliary spines are oriented in such a way as to produce centrifugal currents across the aboral surface leading away from the center and towards the margins and lunules. On the oral surface the ambulatory spines have a thin ciliation at the base while the non-ambulatory spines have dense ciliation at the base producing a strong current. The ciliation of the miliary spines of the food tracts is similar to aboral miliary spines. At the margins of the oral surface the spines are oriented so as to drive currents in towards the center. In the food tracts they produce currents towards the mouth in the radial tracts and laterally towards the ambulacral grooves in the remainder. Over the rest of the ambulacral areas the currents drive towards the adjacent ambulacral grooves.

Feeding Behavior

M. sexiesperforata is a microphagous feeder. Removal and microscopal examination of the food cord passing along the ambulacral groove shows that most particles are less than 20 μ in diameter and in a high proportion of them are of the order of 1 μ in diameter. Within these size limits there appears to be no selection of different types of food—algal cells, detrital particles and sand grains are all collected. Larger particles are sometimes collected and sand grains which only just fit in the groove have been seen passing along it and entering the mouth.

An active animal ploughs slowly through the surface sand always keeping the anterior end (Loven's Ray III) forward. As it moves it builds up a small wall of sand in front of itself, the sand grains of which constantly fall down on the aboral surface where they are carried slowly backwards on the tips of the club-shaped spines. This movement of sand appears to be oriented posteriorly across the aboral surface without special reference to the lunules, but small sand grains which reach the margins of the lunules are carried down through them; larger particles are carried off the posterier margin of the test. Particles entering the lunule usually do not drop through it, but are lowered slowly down by means of the spines and then deposited back in the substratum; during this time they may be actively probed by podia in the lunule, suggesting that the latter may remove from it minute absorbed particles.

If carmine particles instead of sand are placed on the aboral surface of the animal a further process of selection may be observed. Larger particles are treated exactly as sand and it can also be seen that the very small particles (visible only under the microscope) drop down between the club-shaped spines and are carried away by the ciliary currents around the spines. At this lower level some particles travel to the margin of the test and then around it to the oral surface, other particles are carried to the lunules and pass down through them and onto the food tracts on the oral surface. By placing carmine particles in the food tracts of an inverted animal it can be shown that the ciliary currents lead to the ambulacral grooves, except in the radial tract where they lead directly to the mouth. Carmine particles placed on the aboral surface of an animal appear in the ambulacral grooves in a few moments. In the ambulacral groove food can be seen to be loosely aggregated in mucus but the precise point at which the mucus is secreted is still in doubt. As pointed out above the miliary spines of the aboral surface are the most probable site of mucus secretion. In the ambulacral groove the food is carried along by podia and not by cilia.

In summary, then, an animal ploughing through the sand pushes sand onto the aboral surface where it is crudely sorted, large particles being carried along on the tips of the club-shaped spines and ultimately deposited back in the sand either through the lunules or off the posterior edge of the test. Fine particles fall down between the bases of the spines where they are carried away by ciliary currents through the lunules to food tracts on the oral surface. From the food tracts cilia carry them to the ambulacral groove thence to the mouth in a mucus aggregation carried along by podia.

There remains the question of food collection by the podia. Because they are confined to the oral surface it is difficult to see them in normal function, but following the method of Nichols (1959) I have examined them in a perspex box with the aid of a prism and a binocular microscope. Under these circumstances the podia at the margin are seen to be constantly extending and contracting and probing the surroundings of the animal. If carmine particles or yeast stained in congo red are pipetted around the margin, particles may sometimes be seen to be picked up by the podia and drawn in to the margin of the animal where they are released and carried inwards by the ciliary currents. At the same time many podia are seen to extend and contract with no visible particles attached. However, only relatively small magnifications ($\times$ 30) can be used successfully in examining with the prism and I believe that the principal function of these podia is to probe the surrounding sand for very small particles of food, *i.e.*, particles of about 1 μ diameter. Mention has already been made of the manner in which sand grains are probed by podia as they pass down through the lunules. In the perspex box only a few scattered grains of sand can be included with the animal; otherwise they obscure it from view. The animal thus rests directly on the bottom of the box and only the marginal podia, which extend laterally, can be extended effectively. It seems certain, however, that under normal conditions the podia of the oral surface all probe the sand in the same way, collecting small food particles.

Defecation

In an animal such as *M. sexiesperforata* in which the anus is in close proximity to the mouth, special precautions are required to ensure that feces do not re-enter the mouth. Although many animals have been examined from time to time defecation has only been observed on a very few occasions and it appears that it must be an intermittent and not a continuous process.

Defecation commences with a pumping action of the anal papilla followed by cessation of feeding activity; passage of the mucus cord in the ambulacral groove stops completely. The spines between the mouth and the anus beat gently away from the mouth and over the anus, and all around this area pedicellariae become intensely active. The tip of the anus is directed towards the anal lunule and feces are ejected in intermittent puffs of loose particles and not in a mucus string. Examination of a defecating animal from below shows that feces are not, as might be expected, carried up through the anal lunule and so removed in water currents. They fall down from the animal and must in normal circumstances be deposited back in the sand in which the sand dollar community is feeding.

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Summary

1. A brief description of *Mellita sexiesperforata* is given and the process of food collection and defecation are described.

2. Sand pushed onto the aboral surface is sorted by club-shaped spines. Fine particles drop down between the spines and are carried round to the oral surface by ciliary currents, thence to the ambulacral grooves. Mucus is probably secreted by the miliary spines on the aboral surface; podia play an accessory role in food gathering.

3. Defecation is an intermittent process and feeding stops while it is in progress. Spines and pedicellariae prevent feces from reaching the mouth.

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